

PHENETIC ANALYSIS OF *ARCTOSTAPHYLOS PARRYANA*  
I. TWO NEW BURL-FORMING SUBSPECIES

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ABSTRACT

*Arctostaphylos parryana* Lemmon is here circumscribed as a species that includes both non-burl forming and burl-forming taxa. Principal components analysis based on 50 phenetic characters was used to support the recognition of two new subspecies. *Arctostaphylos parryana* subsp. **tumescens** Keeley, Boykin, & Massihi is morphologically similar to the nominate subspecies but is distinct in its geographical and ecological distribution, presence of a globose basal burl and erect growth form. *Arctostaphylos parryana* subsp. **deserticum** Keeley, Boykin, & Massihi also differs from the nominate subspecies in the presence of a basal burl, and differs from both other subspecies in its intensely glaucous, slightly narrower leaves and smaller fruits and desert chaparral habitat. These subspecies increase the range of *A. parryana* by >150 km southeastward, and to the San Bernardino, San Jacinto, Santa Rosa, and San Ysidro mountain ranges and to Riverside and San Diego counties.

As presented in previous taxonomic treatments, *Arctostaphylos parryana* Lemmon is a polyploid, non-burl forming manzanita with a mounded growth form (Fig. 1) and typically is distributed as scattered shrubs in arid woodlands and montane forests (Adams 1940, Wells 1993). It ranges from Lockwood Valley and Mt. Pinos in eastern Ventura County to the southern Tehachipi Mountains of Kern County and northern and eastern portions of the San Gabriel Mountains in Los Angeles and San Bernardino counties. It is morphologically distinguished by its tomentose branchlets and rachises, reduced floral bracts, and round fruits with a solid endocarp stone. Recently we have made extensive collections of manzanitas with these characteristics, indicating clear affinities to *A. parryana*, and in this paper we will show

- (1) A significant increase in the range of this species east and south,



FIG. 1. Mounded growth form of typical *A. parryana*.

- (2) that the species includes many burl-forming populations,
- (3) these populations are best treated as subspecies, and in a subsequent contribution (Keeley et al. in preparation) we will show
- (4) The pattern of variation in *A. parryana* suggests the hypothesis that there has been widespread hybridization and introgression from *A. glandulosa* Eastwood, and
- (5) evidence that *A. gabrielensis* Wells comprises a single population along a cline from *A. parryana* to *A. glandulosa*.

#### STUDY SITES

Distribution of taxa considered here is shown in Figure 2 and names, locality data, and sample sizes are in Table 1. Here the term "population" is used broadly to refer to both distinct populations as well as metapopulations (groups of populations separated by areas of unsuitable habitat).

#### METHODS

Extensive collections of all populations were made in late summer and autumn in order to obtain both current-year fruits and nascent inflorescences for the following year. These are critical characters in manzanita taxonomy and only specimens with both present were included in our phenetic analysis. The combined presence of these two characters was a determining factor in the final sample size for

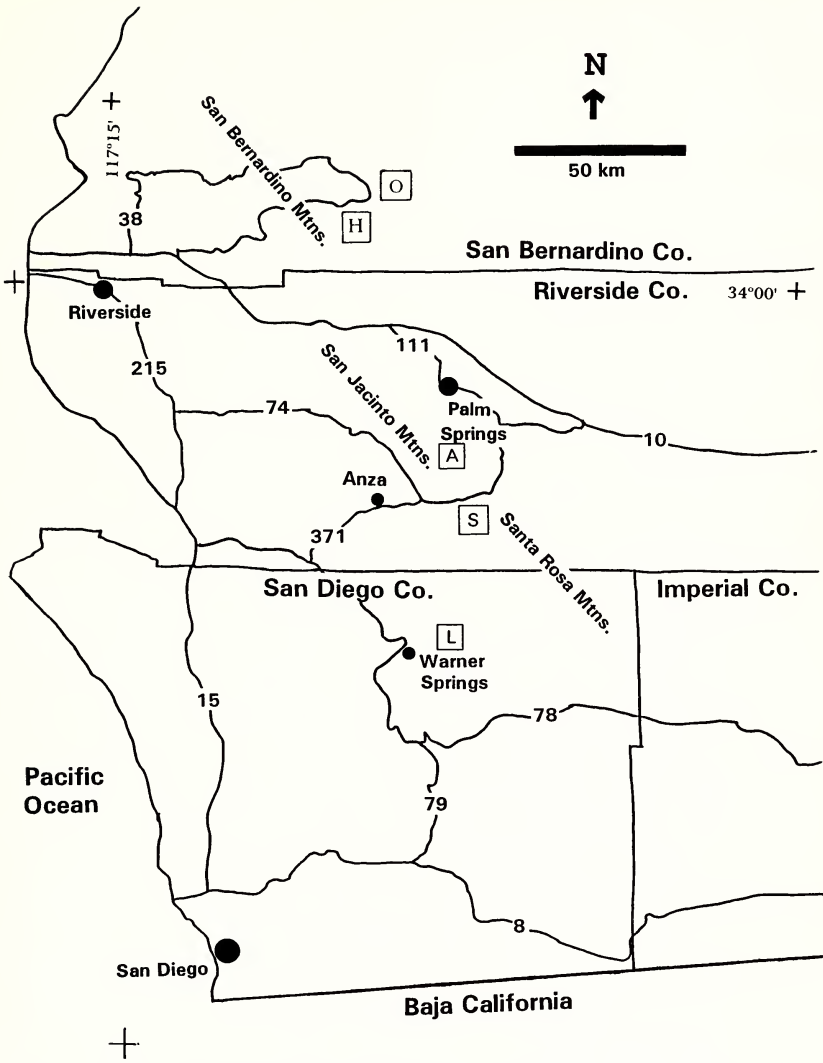


FIG. 2. Eastern distribution of populations studied here. See Table 1 for location data and sample sizes.

each population. A total of 50 characters were recorded for each plant sample, which were subsequently retained as vouchers and deposited at RSA. Fifteen quantitative, 2 meristic, and 30 qualitative characters, and 3 calculated ratios were recorded from each specimen. Qualitative characters were ranked from 1 to 5. Quantitative characters were represented by the mean of two samples from each

TABLE 1. POPULATIONS OF ARCTOSTAPHYLOS INCLUDED IN THIS STUDY.

	Code	Sample size	Burl	County or Country	Mtn. Range	Location	Elevation (m)
<i>A. parryana</i>							
"Ventura"	v	39	No	Ventura/Kern	Tehachapi & Mt. Pinos region	Lockwood Valley Mutau Flat Mt. Pinos	1500-1700 1500-1700 1900
"San Gabriels"	g	68	No	Los Angeles & San Bernardino	San Gabriel	Cero Noroeste Sulphur Spgs. Wrightwood Pacifico	1900-2400 1600-1700 2000 2000
"Onyx"	o	59	No	San Bernardino	San Bernardino	Crystal Lake San Antonio Cyn NE Onyx Peak	1850 1900 2400
"Heartbar"	H	58	Yes	San Bernardino	San Bernardino	Rattlesnake Cyn	2100
"Andreas"	A	20	Yes	Riverside	San Jacinto	SW Heartbar Pk	2100-2300
"Santa Rosa"	S	66	Yes	Riverside	Santa Rosa	Andreas Cyn	2000-2100
"Los Coyotes"	L	30	Yes	San Diego	San Ysidro	N/W Sta. Rosa Mtn. Borrego-Palm Cyn Indian Cyn	1600-2200 1300-1700
<i>A. peninsularis</i>	R	20	Yes	Baja California	San Pedro Martir	W of National Park	1000-2000
<i>A. glandulosa</i>	C	30	Yes	San Diego	San Marcos	Encinitas-Econdido	100-500

specimen. All character states were standardized by transforming each variable with a z-score obtained by subtracting each observation from the mean of all individuals, and dividing by the standard deviation. This data matrix was used for ordination with principal components analysis using SYSTAT for Windows, Version 5.05 (Evanston, IL).

Stomatal density on ad- and abaxial surfaces were determined on a sub-sample from each population from epidermal peels made of clear nail polish and examined under 40 $\times$ . Since there was relatively little inter-population variability these data were not taken from every specimen and were not used in the principal components analysis. Chromosome counts were made on some populations from flower buds collected in late winter to early spring and preserved in 3:1 ethanol:glacial acetic acid. Anthers, not yet pigmented, were dissected out and squashed with aceto-carmin and examined at 100 $\times$ . This character was likewise not used in the principal components analysis. Additionally, characters with zero variance were automatically excluded from the principal components analysis.

## RESULTS

*San Bernardino Mountains.* Although previously unrecorded from this range, there is an extensive population of *A. parryana* between 2100 and 2300 m on the western and southern slopes of Heartbar Peak (Table 1 and Fig. 2). These plants are approximately 80 km E of the known range of *A. parryana* in San Antonio Canyon in the San Gabriel Mountains. They are clearly related to *A. parryana* in their bright green foliage, tomentose branchlets and rachises, and relatively large round glabrous fruits with a solid stone (Fig. 3). However, the Heartbar Peak population differed significantly in that each shrub had a well-developed basal burl and lacked the mounded growth form of typical *A. parryana*. Further, the population covered several hectares of densely packed erect manzanitas in association with other chaparral shrubs. This contrasts sharply with the mounded growth form and scattered distribution in woodland and forest gaps, typical of non-burl forming *A. parryana*. The Heartbar population is largely restricted to chaparral on steep slopes and is replaced by *A. patula* in forest gaps in the valley bottom.

Principal components analysis comparing the phenetic traits (excluding the burl and growth form characters) of this Heartbar Peak population (H) with typical *A. parryana* from Ventura County (v) and the San Gabriel Mountains (g) (see Table 1 for location data) verifies the morphological similarity between the newly discovered Heartbar population and typical *A. parryana* (Fig. 4). Although these populations overlapped a great deal, there was some separation along the factor 1 axis, which accounted for 11% of the total vari-





FIG. 3. Large round glabrous fruits of the Heartbar *A. parryana*.

ance. Based on the component loadings, which indicate the extent each character contributes to the variance, the primary difference between these populations was the slightly sparser pubescence and somewhat larger fruits in the Heartbar population. Despite the phenetic similarity, the Heartbar manzanitas were clearly distinguishable from typical *A. parryana* by the prominent basal burl, erect growth habit, and affinity for chaparral.

On the eastern face of the San Bernardino Mountains, between 2100 and 2400 m, a widely scattered population of non-burl forming *A. parryana* was also collected, E of Onyx Peak and extending several km N to Rattlesnake Canyon (Table 1 and Fig. 2). As with

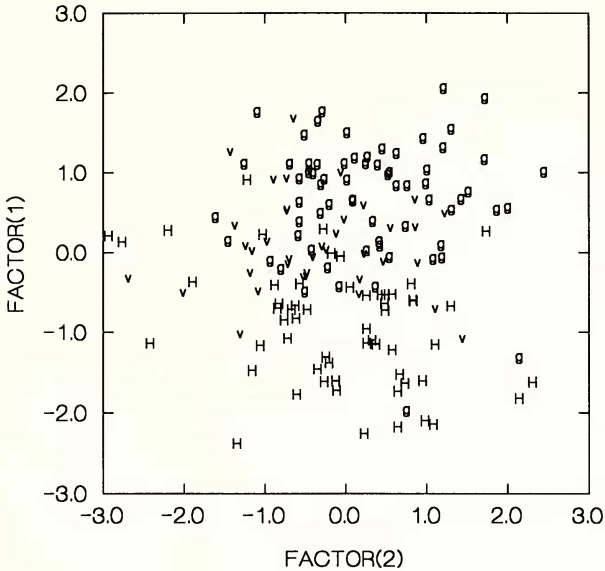


FIG. 4. Plot of the first two factors in the principal component analysis comparing the burl-forming Heartbar manzanitas (H), and typical non-burl-forming *A. parryana* from Ventura County (v) and the San Gabriel Mountains (g). See Table 1 for locations and sample sizes and Table 2 for factor 1 loadings, which explained 11% of the total variance.

typical *A. parryana*, these plants had a mounded growth form and generally were associated with pinyon-juniper woodland. Principal components analysis showed that these manzanitas (o) were largely indistinguishable from typical *A. parryana* from Ventura County (v) and the San Gabriel Mountains (g) (Fig. 5). Separation along the factor 1 axis accounted for 12% of the total variance, primarily contributed by slightly larger fruits in the Onyx populations. Otherwise, this population greatly resembled typical *A. parryana*, however, it represents approximately a 100 km eastward range extension for *A. parryana*.

*San Jacinto, Santa Rosa, and San Ysidro ranges.* Burl-forming manzanitas with tomentose branchlets, reduced floral bracts, and round solid fruits, indicating affinities to *A. parryana*, are also found in three mountain ranges south of the San Bernardino Mountains (Table 1 and Fig. 2). All of these populations occur in chaparral near the desert edge and many are accessible only by trail.

The most extensive populations we have found to-date are at the northern end of the Santa Rosa Mountain Range (Riverside County), between 1600 and 2200 m, on the western and northern sides of Santa Rosa Mountain. Principal components analysis (not shown)

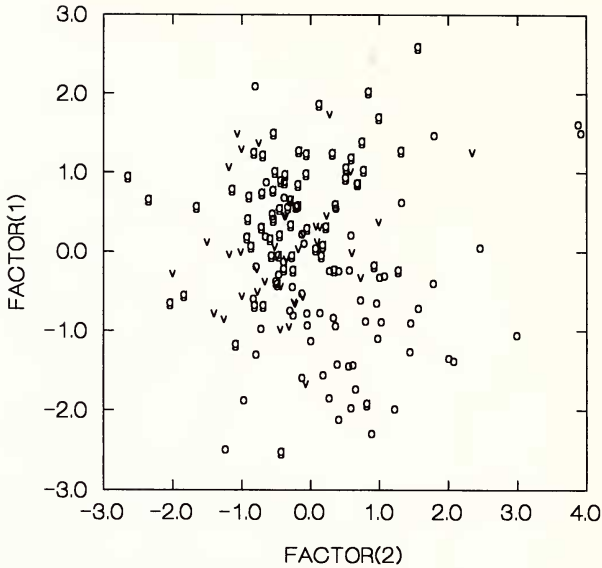


FIG. 5. Plot of the first two factors in the principal component analysis comparing the non-burl-forming *A. parryana* populations from Ventura County (v), San Gabriel Mountains (g), and E of Onyx Peak in the San Bernardino Mountains (o). See Table 1 for locations and sample sizes and Table 2 for factor loadings; factor 1 explained 12% of the total variance.

of four widely separated populations on Santa Rosa Mountain indicated extensive morphological overlap between these populations, thus all populations were treated together as a metapopulation.

Principal components analysis showed that the burl-forming Santa Rosa Mountain (S) manzanitas are well separated from the non-burl forming Ventura (v) plants and overlap slightly with the burl-forming Heartbar (H) plants (Fig. 6). The Santa Rosa Mountain manzanitas share with the Heartbar plants the erect habit and basal burl but differ in having markedly smaller fruits and a preponderance of plants with very glaucous-white leaves, as indicated by the component loadings (Table 2). Overlap between the Santa Rosa Mountain and Heartbar populations (Fig. 6) is due to weakly glaucous shrubs at the higher elevations on Santa Rosa Mountain.

Other extensive burl-forming populations with affinities to *A. parryana* occur further south in the San Ysidro Mountains on the eastern border of the Los Coyotes Indian Reservation in San Diego County (L). These plants appear similar to the Santa Rosa Mountain plants but are strikingly unlike the Heartbar plants in their intensely glaucous and narrower leaves and smaller fruits. Principal components analysis indicates that the Los Coyotes populations are clearly separable from the



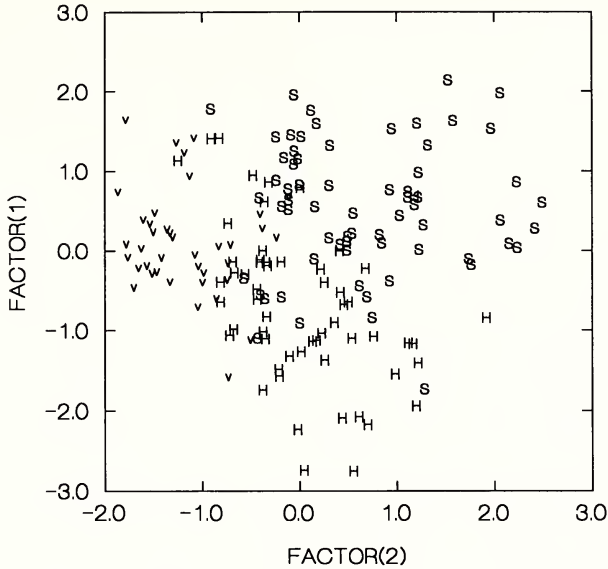


FIG. 6. Plot of the first two factors in the principal component analysis comparing the burl-forming Santa Rosa Mountain population (S) with the burl-forming Heartbar (H), and non-burl-forming Ventura County (v) and the San Gabriel Mountains (g) *A. parryana*. See Table 1 for locations and sample sizes and Table 2 for factor 1 loadings, which explained 10% of the total variance.

typical non-burl-forming *A. parryana* from Ventura County and distinct from the burl-forming *A. parryana* from Heartbar in the San Bernardino Mountains (Fig. 7). The factor 1 axis accounts for 17% of the total variance and component loadings indicate that shorter bract length and greater leaf glaucousness and scabrousness are most significant in separating these populations (Table 2).

Burl-forming *A. parryana* also occur on the desert slopes of the San Jacinto Mountains. One population from Andreas Canyon (A) more resembled Santa Rosa and Los Coyotes plants than San Bernardino plants. Principal components analysis (not shown) indicated that these manzanitas were clearly separable from the Heartbar population and Ventura County population, and the factor 1 axis accounted for 21% of the total variance.

*Comparison with other Arctostaphylos species.* Several characteristics of these burl-forming *A. parryana* populations, e.g., round glabrous fruits with solid stones and glaucous leaves, burls, and desert affinity in some, are shared with the northern Baja California *A. peninsularis* Wells. These *A. parryana* populations also share the burl-forming habit with the widespread coastal range species *A. glandulosa*. Principal components analysis comparing the burl-form-

TABLE 2. CHARACTERS USED IN PRINCIPLE COMPONENTS ANALYSIS AND COMPONENT LOADINGS FOR FACTOR 1 FOR FIGURES 4, 5, 6, 7, &amp; 8. N.I. = not included.

Character	Fig. 4	Fig. 5	Fig. 6	Fig. 7	Fig. 8
Burl	N.I.	N.I.	0.193	0.284	N.I.
Leaf blade length	-0.132	-0.090	-0.154	0.243	0.356
Leaf blade width	0.066	0.425	-0.415	-0.188	-0.005
Ratio leaf width/length	-0.219	-0.512	0.370	0.462	0.430
Basal angle	-0.141	-0.474	0.128	0.260	0.218
Apical angle	-0.156	-0.431	0.221	0.347	0.240
Blade shape	0.053	-0.327	0.076	-0.214	0.036
Petiole length	-0.250	0.061	-0.026	0.192	0.026
Leaf color	-0.570	-0.394	0.178	0.315	0.410
Leaf glaucousness	0.003	-0.158	-0.571	-0.816	-0.088
Leaf scabrousness	-0.302	-0.143	0.399	0.770	0.593
Branchlet pubescence	-0.651	-0.550	0.378	0.764	0.890
Petiole pubescence	-0.624	-0.572	0.190	0.682	0.881
Leaf blade pubescence					
Mature leaf	-0.307	-0.207	0.432	0.300	0.765
Immature leaf	-0.311	-0.309	0.205	0.579	0.812
Rachis pubescence	-0.576	-0.467	0.380	0.728	0.850
Pedicle pubescence	-0.037	-0.081	0.321	0.612	0.817
Branchlet glandularity	0.503	0.232	0.151	0.476	0.885
Petiole glandularity	0.147	-0.023	0.187	0.587	0.910
Leaf blade glandularity	N.I.	N.I.	0.185	0.182	0.843
Rachis glandularity	0.464	0.163	0.183	0.258	0.876
Pedicle glandularity	0.176	N.I.	0.377	0.466	0.887
Inflorescence length	0.063	0.201	0.154	0.020	0.237
# of rachis branches	0.513	0.269	-0.132	-0.142	-0.023
Bract spacing	0.503	0.176	-0.245	-0.156	-0.042
Bract keel	0.127	0.289	0.057	0.185	-0.602
Bract shape	0.166	0.132	-0.057	-0.236	-0.781
Bract marcescence	-0.417	-0.301	-0.287	0.239	-0.276
Bract reflexed	-0.079	-0.093	-0.037	0.407	0.574
Bract length, subtending					
Inflorescence	-0.128	0.170	0.609	0.851	0.622
Flower bud	-0.329	-0.139	0.161	0.104	0.674
Pedicle length	-0.269	0.160	0.011	0.480	-0.037
Sepal shape	-0.364	-0.296	0.420	-0.015	-0.617
Sepal reflexed	0.071	0.022	0.342	0.487	-0.119
Fruit color	0.084	-0.033	-0.003	0.517	-0.170
Fruit height	0.307	0.525	-0.519	-0.406	-0.727
Fruit width	0.477	0.599	-0.607	-0.305	-0.438
Fruit width/fruit height	0.147	0.061	-0.103	0.200	0.585
Fruit weight	0.477	0.700	-0.706	-0.482	-0.597
Fruit pubescence	0.181	0.094	0.044	0.588	0.486
Fruit glandularity	N.I.	N.I.	0.171	0.267	0.723
Pericarp weight	0.453	0.530	-0.399	-0.277	-0.507
Endocarp weight	0.469	0.599	-0.707	-0.493	-0.541
Endocarp height	0.400	0.466	-0.472	-0.159	-0.677
Endocarp width	0.510	0.566	-0.661	-0.322	-0.563
Endocarp apiculate	-0.229	-0.199	-0.011	-0.089	-0.590
Mesocarp texture	0.170	0.174	-0.115	-0.157	-0.370
Endocarp segments	-0.305	-0.286	0.128	0.296	0.710
Endocarp lateral ridges	-0.433	-0.463	0.027	0.063	-0.190
Endocarp sculpturing	-0.287	-0.332	0.035	0.016	-0.439

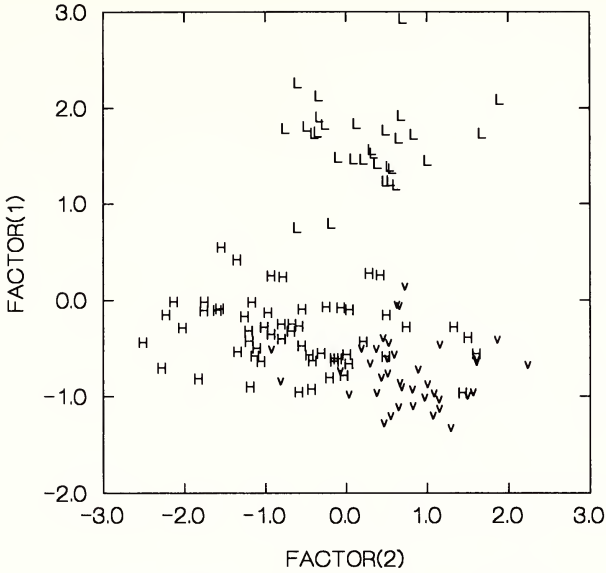


Fig. 7. Plot of the first two factors in the principal component analysis comparing the burl-forming Los Coyotes population (L) with the burl-forming Heartbar (H), and non-burl-forming Ventura County (v) *A. parryana*. See Table 1 for locations and sample sizes and Table 2 for factor 1 loadings, which explained 17% of the total variance.

ing *A. parryana* taxa (H,A,S,L) with burl-forming *A. peninsularis* (R) from the San Pedro Mártir and *A. glandulosa* (C) from the coastal ranges of San Diego County is shown in Figure 8. The strongest separation was on the factor 1 axis, which accounted for 33% of the variance and illustrates that these *A. parryana* taxa are clearly distinct from *A. glandulosa* and *A. peninsularis*, based largely on indument and fruit characters (Table 2).

**Chromosome number.** Two chromosome counts on the burl-forming Heartbar *A. parryana* gave counts of  $n = 26$ , indicating they were tetraploid. Two counts for non-burl-forming Onyx Peak and Rattlesnake Canyon specimens likewise gave counts of  $n = 26$ , and one count for a Santa Rosa Mountain plant gave a count of  $n = 26$ . Three counts for Los Coyotes plants gave both  $n = 13$  and  $n = 26$ .

#### DISCUSSION

These studies greatly change our perception of *A. parryana*, in terms of its geographical range, ecology, and range of phenetic variation. The Heartbar population is morphologically quite close to the type, although fruits are somewhat larger (Fig. 3). This population

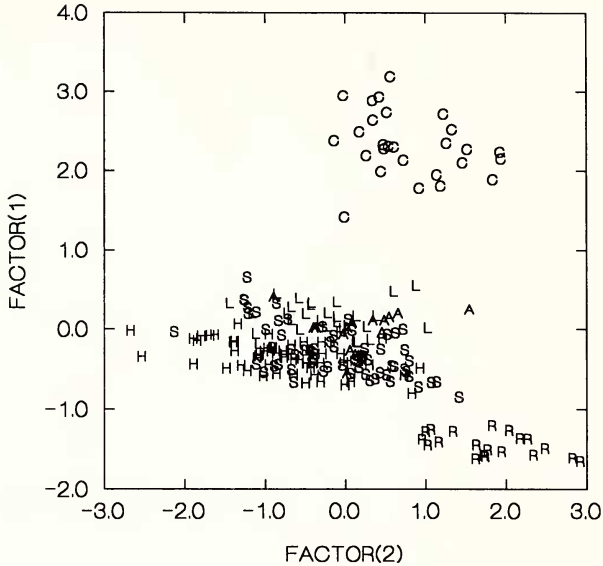


FIG. 8. Plot of the first two factors in the principal component analysis comparing the burl-forming populations of *A. parryana* (H = Heartbar, S = Santa Rosa, L = Los Coyotes, A = Andreas Cyn) with the burl-forming *A. glandulosa* (C) and burl-forming *A. peninsularis* (R). See Table 1 for locations and sample sizes and Table 2 for factor 1 loadings, which explained 33% of the total variance.

is markedly unlike typical *A. parryana* in having a well-developed basal burl, an erect growth form and distribution in dense montane chaparral. This contrasts markedly with *A. parryana* throughout its range where it is a non-burl-forming shrub with a mounded growth form (Fig. 1) and is distributed as scattered shrubs, in pinyon-juniper woodland or mixed conifer forests. We believe these differences are significant and the San Bernardino Mountains burl-forming plants should be recognized at the level of subspecies.

Burl-forming *A. parryana* in the ranges south of the San Bernardino Mountains are, however, phenetically quite distinct from the Heartbar population, most prominently in their intensely glaucous foliage, and they also have slightly narrower and more pointed leaves, and smaller fruits. Additionally, this taxon is ecologically distinct in its restriction to chaparral on the desert edge of the San Jacinto, Santa Rosa, and San Ysidro mountains. Therefore, we propose these glaucous-leaved manzanitas be treated as an additional subspecies.

#### TAXONOMIC TREATMENT

***Arctostaphylos parryana* subsp. *tumescens*** J. Keeley, Boykin, & Massihi, subsp. nov.—TYPE: USA, California, San Bernardino

County, chaparral covered slopes on NW face of Heartbar Peak, S of Hwy 38, 2160 m, San Bernardino Mountains, 34°10', 116°45', 23 Sept 1992, *J. Keeley & M. Keeley 21436* (holotype, RSA; isotypes, CAS, SD, MO).

Frutices erecti, caudex tumescens, repullulans post combustum; drupae 10 mm diametro.

Erect shrub with large globose burl formed early in development and platform-like on older resprouted shrubs, in chaparral habitat. Fruits 10 mm diameter. *n* = 26 (A. Massihi and J. Keeley). The epithet recognizes the swollen basal burl.

Montane chaparral in eastern San Bernardino Mountains, from Heartbar Peak east, and in the San Gabriel Mountains, such as chaparral near Newcomb Ranch (*J. Keeley 20599*, RSA).

*Paratypes*. USA, California, San Bernardino County, Rd to Coon Crk., 5.0 km SE of Hwy 38, southern base of Heartbar Peak, 2310 m, 27 Sept 1992, *J. Keeley 21864* (RSA); ecotone of chaparral and *Quercus chrysolepis* woodland, SE face of Heartbar Peak, 2250 m, 25 October 1992, *J. E. Keeley 22305* (RSA).

***Arctostaphylos parryana* subsp. *deserticum*** J. Keeley, Boykin, & Massihi, subsp. nov.—TYPE: USA, California, San Diego County, Middle Fork Borrego Palm Cyn., 3–4 km SE San Ignacio, E of Hot Springs Mountain, 1500 m, San Ysidro Mountains, 33°17', 116°30', 26 Sept 1992, *J. Keeley 21656* (holotype, RSA; isotypes, CAS, SD, MO).

Frutices erecti, caudex tumescens, repullulans post combustum; laminae glaucae, ellipticae, apices acuti; drupae 7–8 mm diametro.

Erect shrub with large globose burl formed early in development and platform-like on older resprouted shrubs, in chaparral near desert edge. Leaf blades narrow-elliptic with acute apices and moderately to intensely glaucous, fruits 7–8 mm diameter. *n* = 13, 26 (A. Massihi and J. Keeley). The epithet recognizes the consistent tendency of this taxon to be restricted to the desert edge of chaparral.

Chaparral at desert edge in San Diego and Riverside counties.

*Paratypes*. USA, California, San Diego County, Los Coyotes Indian Reservation, Indian Canyon, E. of Warner Springs, 1320 m, 10 April 1994, *Massihi, J. Keeley 25300* (RSA); S facing slopes E of Hot Springs Mountain, upper end of Choke Cherry Valley, Los Coyotes Indian Reservation, 1670 m, 18 September 1992, *J. Keeley 21326* (RSA); Riverside County, Road to Santa Rosa Mountain (7SO2), 2.5 km S of Hwy 74, 1640 m, Santa Rosa Mountains, 32°00', 116°30', 16 July 1992, *J. Keeley 16636* (RSA).

TABLE 3. *ARCTOSTAPHYLOS PARRYANA* SUBSPECIES COMPARISON. Mean  $\pm$  standard error. Glaucous scale: 1 = intensely glaucous - 5 = non-glaucous and lustrous. Scabrous scale: 1 = smooth - 5 = rough.

Character	<i>A. parryana</i> ssp. <i>parryana</i>	<i>A. parryana</i> ssp. <i>tumescens</i>	<i>A. parryana</i> ssp. <i>deserticum</i>	<i>A. glandulosa</i> (coastal San Diego)	<i>A. peninsularis</i> (San Pedro Martir)
Sample size	107	58	30	33	20
Chromosome #	$n = 26$	$n = 26$	$n = 13, 26$	$n = 26$	?
Burl	No	Yes	Yes	Yes	Yes
Leaves					
Length	$32 \pm 1$	$32 \pm 1$	$33 \pm 1$	$37 \pm 1$	$32 \pm 1$
Length/width	$1.6 \pm 0.0$	$1.5 \pm 0.0$	$1.7 \pm 0.0$	$1.8 \pm 0.1$	$1.7 \pm 0.0$
Apical angle	$39 \pm 1$	$34 \pm 1$	$44 \pm 1$	$46 \pm 2$	$44 \pm 1$
Glaucous	$4.1 \pm 0.1$	$4.0 \pm 0.1$	$2.1 \pm 0.1$	$2.8 \pm 0.1$	$1.3 \pm 0.1$
Scabrous	$1.2 \pm 0.1$	$1.0 \pm 0.1$	$2.2 \pm 0.1$	$2.6 \pm 0.2$	$1.0 \pm 0.0$
Stomata					
Abaxial density (#/mm <sup>2</sup> )	$24 \pm 0$	$25 \pm 0$	$21 \pm 0$	$27 \pm 1$	$25 \pm 1$
Ratio abaxial/adaxial	$1.0 \pm 0.0$	$1.1 \pm 0.0$	$1.0 \pm 0.0$	$1.4 \pm 0.1$	$1.2 \pm 0.1$
Branchlet indument	Tomentose	Tomentose	Tomentose	Hirsute Eglandular to intensely glandular	Glabrous
Lower Bract					
Length	$0.4 \pm 0.1$	$0.1 \pm 0.1$	$4.6 \pm 0.2$	$6.3 \pm 0.4$	$0.2 \pm 0.2$
Fruits					
Width/height	$1.0 \pm 0.0$	$1.0 \pm 0.0$	$1.1 \pm 0.0$	$1.5 \pm 0.1$	$1.0 \pm 0.0$
Mass (g)	$383 \pm 9$	$447 \pm 19$	$329 \pm 17$	$145 \pm 10$	$242 \pm 19$
Pyrenes	$1.2 \pm 0.0$	$1.1 \pm 0.0$	$1.3 \pm 0.1$	$3.1 \pm 0.2$	$1.0 \pm 0.0$



## CONCLUSIONS

Table 3 contrasts these newly described subspecies with *Arctostaphylos parryana* ssp. *parryana* and with other morphologically similar burl-forming species. Morphologically, *A. parryana* ssp. *tumescens* is nearly indistinguishable from the nominate subspecies and has diverged largely in habitat, growth form and the presence of a basal burl. Greater divergence is seen in *A. parryana* ssp. *deserticum* with several foliage characteristics tending towards those of *A. glandulosa*, with which it co-occurs on the western edge of its range. However, *A. parryana* ssp. *deserticum* has fruits that are more than double those of *A. glandulosa* and the round, mostly solid endocarp stones clearly distinguish it from that species.

## ACKNOWLEDGMENTS

We thank Nancy James for her early unpublished report of a burl-forming manzanita from Heartbar Peak and Steve Boyd (RSA) for curating these collections.

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